

First report of the Eocene gastropod *Mitrella* (*Bastropia*) (Neogastropoda: Columbelloidea) from the northeast Pacific and paleobiogeographic implications

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ABSTRACT

The columbellid neogastropod *Mitrella* (*Bastropia*) *llajasensis* new species is described from a lower Eocene siltstone bed in the shallow-marine part of the Llajas Formation, Ventura County, southern California. This new species, which lived in a warm-water environment, is the first record of *Bastropia* Palmer, 1937 in the northeast Pacific region. *Bastropia* differs from *Mitrella* Risso, 1826 by having axial riblets on an early part of the spire and a longer and more constricted anterior canal. In addition, the majority of species of *Bastropia* have incised-spiral line(s), with or without pits, near the suture on the posterior part of the lower spire whorls and on the last whorl. The geologic range of *Bastropia* is late Paleocene? (Thanetian?) and early Eocene (Ypresian) to late middle Eocene (Bartonian). Its previous occurrences are in Alabama (oldest occurrence), Texas, and South Island, New Zealand (youngest occurrence). *Bastropia* most likely had planktotrophic larval development, and the introduction of *Bastropia* into California from the Gulf Coast region was closely associated with the “Early Eocene Climatic Optimum” (EEO), a time of global warmth and high sea level.

Additional Keywords: Simi Valley, thermophilic

INTRODUCTION

Neogastropods first became abundant during the Early Cretaceous (late Albian) (Kiel, 2002) and subsequently became increasingly diversified. One of the post-Cretaceous neogastropod groups is family Columbelloidea Swainson, 1840. According to Schnetler (2001), the earliest known columbellids are of Paleocene age, belong to *Astyris*

H. and A. Adams, 1853, and are found in northern Europe and Greenland. The global Paleogene (Paleocene to Oligocene) record of columbellids is meager. In the northeast Pacific, in a region extending from southwestern Washington to southern California, their record is extremely rare. The only Paleogene columbellid reported previously from this particular region is *Mitrella* (*Mitrella*) *blackhillsensis* (Squires and Goedert, 1994), of middle early Eocene age from the Crescent Formation in southwestern Washington. This present study concerns the columbellid *Mitrella* (*Bastropia*) *llajasensis* new species of late early Eocene age from the Llajas Formation in southern California (Figure 1). *Bastropia* Palmer, 1937 is known previously from Eocene strata in Alabama, Texas, and South Island, New Zealand (Table 1).

Columbellids underwent great diversification during the Miocene to Holocene. For example, a great array of columbellids is found in middle Miocene deposits of the Caribbean region (Woodring, 1964: 246). Today, columbellids comprise a highly diverse group with about 400 extant species. Their shells are small, normally between 3 and 20 mm in height. Most columbellids are active epibenthic carnivores or scavengers, but some feed on algae. Herbivory is uncommon among neogastropods, and only the columbellids and nassariine buccinids include herbivorous species. Columbellids today have worldwide distribution, mainly in tropical and warm-temperate seas, but a few species inhabit high-latitude and deep-ocean environments (deMaintenon, 1999: 2008). Columbellids have larval-developmental strategies ranging from embryos hatching into planktotrophic veliger larvae (indirect development) to embryos hatching into small crawling snails (non-pelagic development) (Bandel, 1974). Columbellids can have determinate growth, thus, at adulthood there is thickening of the outer lip, with concomitant development of denticles

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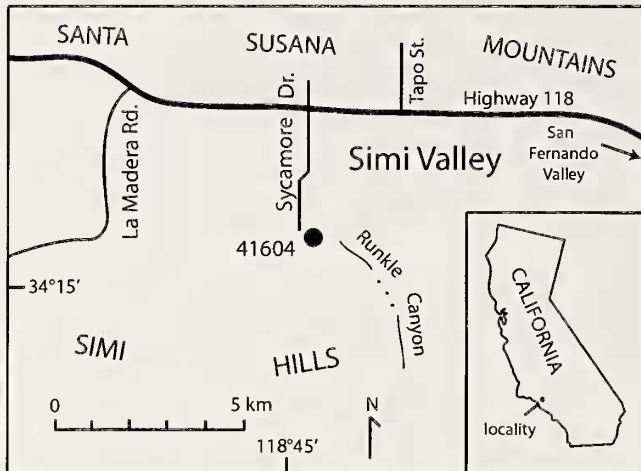


Figure 1. Index map of LACMIP locality 41604, the type locality of the new species.

on the interior surface of the outer lip (deMaintenon, 2005: 501; Pernet, 2007).

MATERIALS AND METHODS

The new species is based on a well-preserved single specimen. Its small size (8 mm height) is most likely why this species has been previously overlooked. Shells of this size are commonly firmly cemented in rock matrix in the Lajas Formation, and, as a result, they are easily destroyed during the process of collecting. In the case of the new species, however, it was found in relatively soft matrix, which was easily removed by picking at the grains with a very sharp, small needle. The lower and middle Eocene provincial molluscan “stages” mentioned in the text are informal (in quotation marks) and, as discussed by Squires (2003), apply mainly to California. Morphologic terms are from Cox (1960). Supergeneric classification is based on Bouchet and Rocroi (2005: 254).

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENT

Squires (1984, 2001) provided details of the stratigraphy, depositional environments, and paleontology of the Lajas Formation. The locality where the new species was found is in siltstone within the middle lower part of the “shallow-marine (transgressive) deposits” in the formation. This part of the formation is of late early

Eocene age. Co-occurring shallow-marine, warm-water species are the large benthic foraminifer *Pseudophragmina (Proporocyclina) clarki* (Cushman, 1920) and the goneplacid crab *Glyphithyreus weaveri* (Rathbun, 1926).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797
Clade Neogastropoda
Superfamily Buccinoidea Rafinesque, 1815

Family Columbellidae Swainson, 1840

Discussion: DeMaintenon (1999, 2008) reported that columbellids have retained the basic neogastropod gut anatomy and that the herbivory observed in columbellids is probably a derived condition. The classification of columbellids is presently not well resolved, with many taxa based on morphologic groups rather than on monophyletic clades (deMaintenon, 1999). Results of deMaintenon’s (1999: 264) parsimony-based phylogenetic studies support a close relationship between columbellids and buccinids.

The supraspecific assignment of Paleogene columbellids has been highly unstable. The historical trend in the literature has been the usage of names belonging to extant genera. As noted by deMaintenon (2008: 267), many extant and fossil species currently are placed in genus *Mitrella* Risso, 1826. DeMaintenon (1999, 2008) reported, however, that *Mitrella* is not a monophyletic group, but it is a polyphyletic collective for biconic columbellids with smooth, unsculptured shells.

Genus *Mitrella* Risso, 1826

Type Species: *Mitrella scripta* (Linnaeus, 1758) [= *Mitrella flaminea* Risso, 1826], by subsequent designation (see Woodring, 1928: 273); extant, Mediterranean Sea, Portugal, and Morocco (Poppe and Coto, 1991: 152).

Description: Shell small (approximately between 4 and 18 mm height), fusiform. Spire moderately high to high, apex subrounded to acicular-like. Protoconch low-domal, paucispiral, smooth. Teleoconch five to eight whorls. Whorls convex to flat-sided. Suture impressed to indistinct. Shell generally smooth, except for pillar (neck) area. Shell can be glossy. Axial sculpture normally absent. Those in modern taxa having rare exceptions of axial riblets on upper spire (see below) need modern systematic work and might represent different genera or subgenera.

Table 1. Ages and geographic distribution of *Bastropia* species.

Species	Age	Location
<i>B. subfraxa</i> (Harris, 1899)	late Thanetian?, early Ypresian	Alabama
<i>B. llajasensis</i> new species	late early Ypresian	Southern California
<i>B. bastropensis</i> (Harris, 1895)	early to middle Lutetian	Texas
<i>B. mackayi</i> (Suter, 1917)	late Lutetian to early Bartonian	South Island, New Zealand

Spiral sculpture prominent on pillar, elsewhere, minor or absent. Aperture on most species wide, short, and truncate. Columella generally straight and smooth with slight callus. Pillar commonly short. Interior of outer lip can have denticles. Area preceding outer lip can have "varix"-like swollen area.

Discussion: Keen (1971) reported two species of *Mitrella* that have axial riblets on the earliest teleoconch whorls. Both species are from the southern tip of Baja California, Mexico. They are *Mitrella baccata* (Gaskoin, 1852) (also see Keen, 1971: fig 1231) and *Mitrella caulerpae* Keen (1971: fig. 1232, two views). *Mitrella baccata* has axial ribs on the first two early teleoconch whorls and has a very short anterior canal. *Mitrella caulerpae* has axial ribs on only the first teleoconch whorl, a moderately short anterior canal, and either a thick outer lip or one with a varix.

Most nominal *Mitrella*, like the extant *Mitrella pallargyi* (Dautzenberg, 1927) in the eastern Atlantic, have been reported as having planktotrophic development, inferred from the multispiral protoconch of this species (see World Register of Marine Species at <http://www.marinespecies.org>). By similar reasoning, Harzhauser and Kowalke (2002) inferred that a Miocene species of *Mitrella* had planktotrophic development. A few extant species of *Mitrella* have been observed as having nonpelagic development (Chaney and deMaintenon, 2009).

Subgenus *Bastropia* Palmer, 1937

Type Species: *Astyris bastropensis* Harris, 1895, by original designation, middle Eocene, Texas.

Description: Shell small (up to 20 mm height), slender fusiform. Spire high. Pleural angle 25° to 40°. Protoconch three smooth whorls. Teleoconch 5 to 6.5 whorls. First one to two teleoconch whorls with many and closely spaced axial riblets. Other spire whorls smooth, but posterior part of penultimate and last whorls can have incised spiral line(s), with or without many closely spaced pits. Columella straight and with slight callus. Aperture narrow and long. Anterior canal well developed and constricted. Pillar elongate and covered by many spiral ribs; those extending onto medial area of columella can create "plicate" appearance. Aperture narrow and long. Anterior canal moderately long to long, anterior canal constricted, siphonal fasciole can be distinct.

Discussion: The type species of *Bastropia* differs from the type species of *Mitrella* by having a narrower last whorl, axial riblets on the first and/or second teleoconch whorls, incised spiral line(s) with or without pits commonly present on posterior parts of the lower spire whorls and on the last whorl, spiral ribs present on base of the last whorl, absence of thick callus on the inner and parietal lips, thinner outer lip, and an aperture that is more distinctly constricted anteriorly. Whether or not there are denticles on the interior of the outer lip of *Bastropia* is unknown because all the specimens of the

all the species of *Bastropia* have the margin of the outer lip broken. All these specimens might be juveniles.

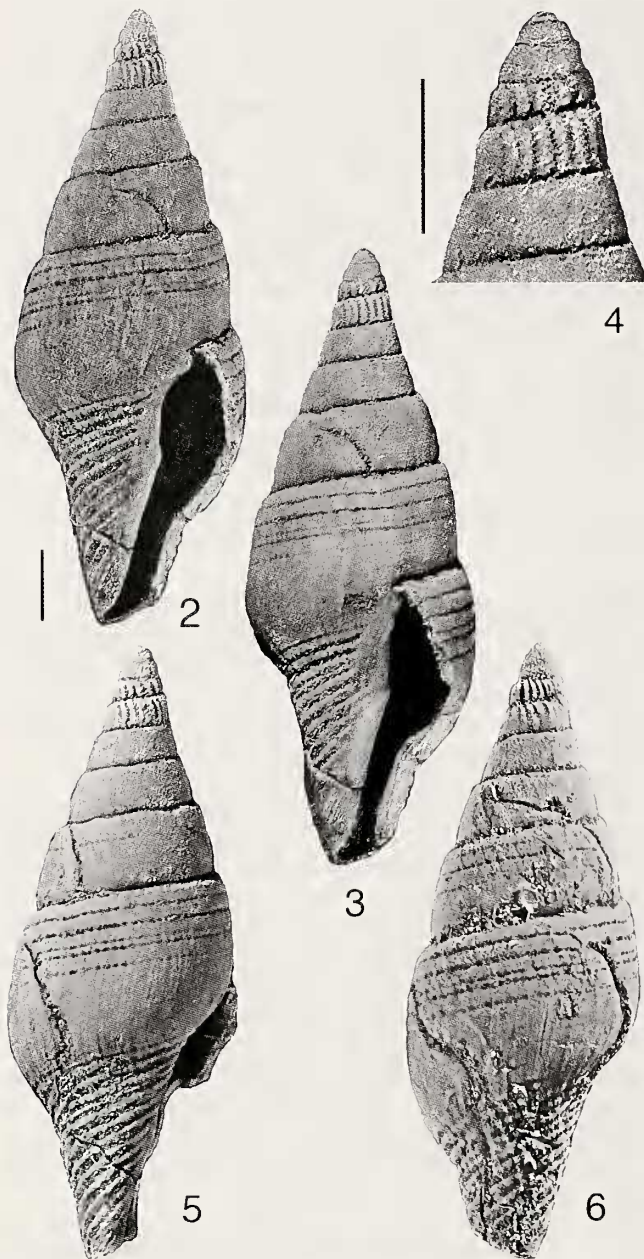
Palmer (1937: 282) stated that the height of the spire of *Bastropia* is greater than the height of its last whorl, but, based on measurements of the four known species of *Bastropia* listed in Table 1, this statement is incorrect. The height of the spire is actually less (in most species, slightly less) than the height of the last whorl. Modern workers have commonly identified (e.g., Palmer, 1937) or compared (e.g., MacNeil and Dockery, 1984) these four species to *Mitrella* (*Bastropia*). Maxwell (1992: 130, fig. 7e) recognized *Bastropia* as a distinct genus, and future work might confirm his assertion. Each species of *Bastropia* is known only from a single specimen or just a few specimens, and all specimens are from siliciclastic sandstone (can be glauconitic) or siltstone.

Bastropia llajasensis new species (Figures 2–6)

Diagnosis: *Bastropia* with a relatively low spire and wide pleural angle (40°), axial riblets on both second and third teleoconch whorls, incised spiral line(s) with or without pits commonly present near lower suture of lower spire whorls and near suture of last whorl, somewhat inflated last whorl, distinct siphonal fasciole.

Description: Shell small (8 mm height, 3 mm diameter), fusiform elongate. Entire shell comprised of nine whorls. Pleural angle 40°. Protoconch three whorls, overall narrowly conical, smooth; apical whorl low and domal with other two whorls slightly convex. Teleoconch six whorls, rather flat-sided except for more convex last whorl. Suture indented, imparting tabulate look to lower spire whorls. Axial sculpture confined to first and second teleoconch whorls (i.e., fourth and fifth whorls of entire shell) and consisting of approximately 18 narrow, closely spaced opisthocyrt riblets extending from suture to suture and general alignment on both sides of suture. Spiral sculpture consisting of line(s) and ribs: Incised-spiral line(s) somewhat irregularly spaced, bearing many closely spaced pits between slightly raised growth lines, and confined to posterior part of penultimate and last whorls (three spiral lines on penultimate whorl and five on last whorl); spiral ribs confined to pillar (base of last whorl). Aperture narrow and long, widest posteriorly and with distinct constriction anteriorly. Outer lip missing. Inner lip with thin callus. Pillar long and with approximately 12 prominent spiral ribs; those on central part of pillar have "plicate appearance" underneath callus and onto inner lip but not extending very far into aperture. Pillar with small but distinct siphonal notch. Siphonal canal not bent. Growth line on spire whorls prosocline; growth line on last whorl parasigmoidal near suture but prosocline on pillar; intersection of growth lines and spiral ribs on pillar near columella producing weak cancellate shell-surface structure.

Holotype: LACMIP (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section) 14514.



Figures 2–6. *Mitrella (Bastropia) llajasensis* new species. Holotype LACMIP 14514, LACMIP loc. 41604, height 8 mm. 2. Apertural view. 3. Apertural view turned slightly left. 4. Closeup of tip (height 1 mm) shown in previous figure. 5. Left-lateral view. 6. Abapertural view. Scale bars = 1 mm.

Type Locality: LACMIP 41604, in greenish-brown siltstone, on north side of paved road leading to a large water tank on east side of mouth of Runkle Canyon, near intersection with Sequoia Street, Santa Susana Quadrangle, 7.5-minute, photorevised 1969, south side of Simi Valley, Ventura County, southern California (Figure 1). Collector: R.L. Squires, March 27, 1999.

Geologic Age: Late early Eocene.

Distribution: Upper Ypresian Stage (equivalent to provincial lower “Domengine Stage”) part of the Llajas Formation, lower middle part within the “transgressive shallow marine” deposits, southern Simi Valley, Ventura County, southern California.

Etymology: Named for the Llajas Formation.

Discussion: A single specimen was found. It shows excellent preservation, except that it has undergone some post-depositional crushing. There are cracks in the shell (see Figure 5), and its outer lip is broken off. It is unfortunate that the interior morphology of the outer lip of the specimen cannot be determined, thus it cannot be determined if it represents a juvenile or an adult.

The new species differs from *Bastropia bastropensis* (Harris, 1895: 74, pl. 8, fig. 2; Palmer, 1937: 283, pl. 37, figs. 1, 7), from the lower middle Eocene Weches Formation in Bastrop County, Texas and also questionably from middle Eocene strata in Mississippi (Palmer and Brann, 1966: 774), by having a smaller shell, wider pleural angle, lower spire, no incised-spiral line anterior to the suture, incised spiral lines with pits near the suture between the penultimate and last whorls, last whorl more swollen, spiral ribs on pillar not as high up on the shell, central part of pillar with a “plicate appearance,” and the presence of a siphonal fasciole.

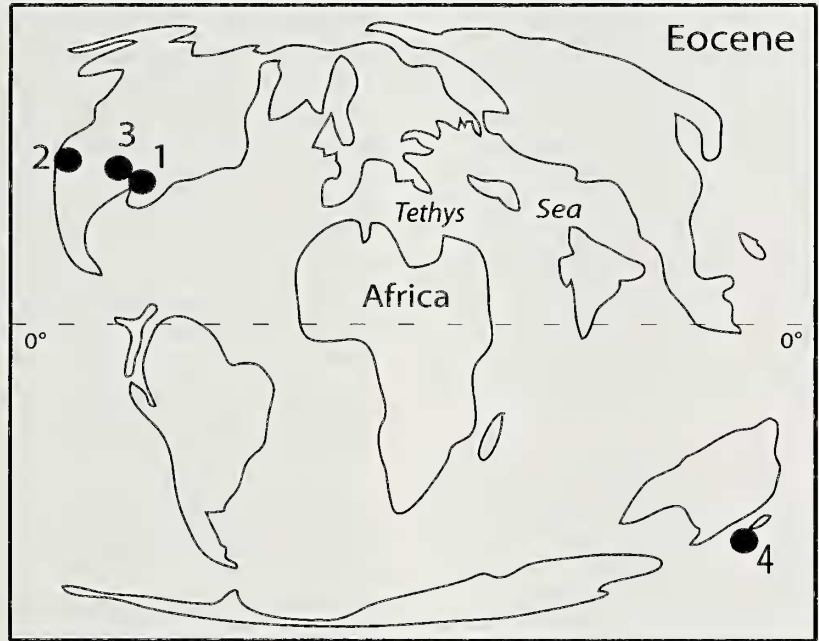
The new species differs from *Bastropia mackayi* (Suter, 1917: 43–44, pl. 5, fig. 12; Maxwell, 1992: 130, fig. 7e), from South Island, New Zealand, by having a smaller shell, wider pleural angle, lower spire, no incised spiral line on ante-penultimate whorl, additional incised spiral lines (but with pits) on last whorl and penultimate whorls, fewer spiral ribs on pillar, shorter posterior part of aperture, more inflated last whorl, and the presence of a siphonal fasciole. According to Maxwell (1992), *B. mackayi* occurs in either upper middle Eocene (upper Lutetian) or upper middle Eocene (Bartonian) strata, thus making *C. (B.) mackayi* the youngest known *Bastropia*.

The new species differs from *Bastropia subfraxa* (Harris, 1899: 58–59, pl. 7, fig. 11), from the lower Eocene (Ypresian) Bashi Member of the Hatchetigbee Formation Member in Alabama (Palmer and Brann, 1966: 512 [as *Astyris subfraxa*]), by having a smaller shell, wider pleural angle, lower spire, presence of spiral sculpture on the posterior part of penultimate and last whorls, and a more inflated last whorl. A questionable occurrence of *B. subfraxa* is from the Tuscahoma Formation, Landing Marl Member, in Alabama (Toulmin, 1977: table 2). According to Dockery (1986: fig. 1), this member is near the late Paleocene (Thanetian)/early Eocene (Ypresian) boundary.

The presence of axial riblets on the upper spire of *Mitrella (Bastropia) llajasensis* new species resembles those on the incomplete paratype of the early Eocene columbellid that Garvie (1996) identified as *Mitrella (Clinurella) nuttalli* (Garvie, 1996: 68–69, pl. 14, fig. 17) from the lower Eocene Marquez Member of the Reklav Formation in Texas. The new species differs from

Garvie's paratype, which consists of only the upper spire, by not having near the suture one or more relatively wide spiral ribs with prominent grooves in the interspaces. On the holotype (an adult specimen) of *M. (C.) nuttalli* (see Garvie, 1996: pl. 14, figs. 15–26), whose uppermost spire whorls have been eroded, these spiral ribs and grooves

become even more prominent on the penultimate and last whorls. *Bastropia llajasensis* new species differs also from the holotype of *M. (C.) nuttalli* by having a narrower shell, incised-spiral lines anterior to the suture, pits on these spiral lines, absence of prominent spiral ribs with sunken (flat-bottomed) interspaces on the



Age (Ma)	Epoch	Stage	1	2	3	4	GLOBAL-CLIMATE EVENTS
			Alabama	Southern California	Texas	South Island, New Zealand	
40	Olig.	Lower					cooling begins
		Up.					
	Eocene	Middle	Bartonian				■
			Lutetian			■	
		Lower	Ypresian	■	■		
60	Paleocene	Up.	?				Early Eocene Climatic Optimum (EECC)
		Mid.					
		Low.					

Figure 7. Global paleobiogeographic distribution and associated ranges of *Bastropia* (plotted in order of first-appearance datum); data derived from Table 1. Geologic time scale, stage ages, and timing of global-climatic events from Gradstein et al. (2012). Land-mass positions from Smith et al. (1994). Numbers at top of columns refer to geographic regions and primary sources of data: 1, Harris (1899), Palmer (1937), and Toulmin (1977). 2, present study. 3, Harris (1895). 4, Maxwell (1992).

anterior half of the last whorl, a more elongate pillar, narrower posterior part of aperture, and a more constricted siphonal canal. Although the outer lip is missing in the new species, the holotype of *M. (C.) nuttalli* has an outer lip interior with denticles. The holotype of *M. (Clinurella) nuttalli* is much more similar to the type specimen of the columbellid identified by Cossmann (1886) as *Mitrella (Columbellopsis) biarata* (Cossmann, 1886: 232–234, pl. 10, fig. 3, two views), from middle Eocene (Lutetian) strata in France. In addition, as noted by Garvie (1996: 68), *M. (Clinurella) nuttalli* is similar to *Mitrella (Clinurella) bucciniformis* (Heilprin, 1879: 213, pl. 13, fig. 7) and *Mitrella (Columbellopsis) mississippiensis* (Meyer and Aldrich, 1886: 43, pl. 38, figs. 16, 17, 21, 22).

The new species differs from the earlier mentioned Baja California species *Mitrella bacata* and *M. caulerpae*, which have axial riblets on the first one or two teleoconch whorls, in the following ways: Elongate-fusiform shell with a long anterior canal that is constricted anteriorly, indented sutures, subsutural-spiral sculpture consisting of pitted, incised-spiral lines on the penultimate and last whorls.

The only other known Paleogene columbellid from the northeast Pacific region is *Mitrella (Mitrella) blackhillsensis* Squires and Goedert (1994: 261, figs. 21–23), based on two specimens, from shallow-marine strata in the middle lower Eocene (“Capay Stage”) Crescent Formation in the Black Hills, Thurston County, southwestern Washington. Both specimens, however, are missing their upper spire, thus positive assignment of this species to a subgenus is not possible until more complete specimens are found. This Washington species is very similar to *Mitrella sensu stricto* in having an unsculptured shell (except for spiral ribs on the pillar), a short anterior canal, denticles on the interior of the outer lip, and a “varix”-like swelling preceding the outer lip. *Mitrella (Bastropia) llajasensis* n. sp. differs from this Washington species by having a large size, more slender shell, indented suture on spire, tabulate appearance to the spire whorls, much longer siphonal pillar, spiral sculpture on the posterior part of the penultimate and last whorls, no posterior channel-like indentation in the aperture, and no indication of a “varix”-like swelling preceding the outer lip.

PALEOBIOGEOGRAPHIC IMPLICATIONS

The details of the geologic range and locale of each of the four known species of *Bastropia* are given in Table 1 and are shown diagrammatically in Figure 7. As discussed earlier, a late Paleocene occurrence of *Bastropia* in Alabama is questionable. The earliest known documented record of this subgenus is early Eocene (middle Ypresian) in Alabama, and by the middle Eocene, it had spread westward into nearby Texas.

From the late Paleocene through middle Eocene, there were pulses of immigration of many shallow-marine, warm-water (thermophilic) mollusks and other

marine organisms into the northeast Pacific region. Most arrived from the Old World Tethyan Sea, Gulf Coast, and Caribbean Sea regions by means of westward-flowing currents that passed through a low-latitude seaway (Squires, 1987). The nearness in time between the earliest confirmed record of *Bastropia*, in the early Eocene in Alabama, and when it showed up in southern California, in the late early Eocene, supports the conclusion that *Bastropia* arrived in southern California from the Gulf Coast. Its dispersal would have been greatly facilitated if its larvae had planktotrophic development. This scenario is likely because its protoconch, which consists of three smooth whorls, is similar to those of previously mentioned (see “Discussion” of genus *Mitrella*) inferred planktotrophic species of *Mitrella* (e.g., the extant *Mitrella pallaryi* and a Miocene species). The southern California arrival of *Bastropia* was closely associated with a warming event called the “Early Eocene Climatic Optimum” (EEOCO), 51–53 million years ago (Figure 7). During this event, global temperature reached a long-term maximum (Zachos et al., 2008), and there was a global-sea-level rise (Miller et al., 2011), which would have expedited the dispersal of marine organisms.

With the exception of a species in South Island, New Zealand, *Bastropia* is restricted to North America. This New Zealand occurrence is of late middle Eocene age (Bartonian) and represents the youngest occurrence of this subgenus. It also provides limited evidence that *Bastropia* had an amphitropic distribution (Figure 7). The route of dispersal that *Bastropia* took to reach New Zealand cannot be determined based on current information.

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